South African Journal of Botany 132 (2020) 338–345

Contents lists available at ScienceDirect

South African Journal of Botany

journal homepage: www.elsevier.com/locate/sajb

Secondary invasion and weedy native species dominance after clearing invasive alien plants in South Africa: Status quo and prognosis

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ARTICLE INFO

Article History:
Received 28 January 2020
Revised 2 May 2020
Accepted 6 May 2020
Available online xxx

Keywords:
Biological invasions
Invasive alien plants
Management
Secondary invasion
South Africa
Weedy native species

ABSTRACT

Clearing invasive alien plants often facilitates secondary invasion and/or weedy native species dominance instead of native biodiversity recovery. Secondary invasion and/or weedy native species dominance in turn can present significant barriers to restoration by hindering the recovery of key native species. The problem of secondary invasion and weedy native species dominance is ubiquitous and well appreciated globally, but poorly understood in the context of restoration ecology in South Africa. This study uses a two-pronged approach – a literature review plus an expert workshop – to evaluate the knowledge on secondary invasion and/or weedy native species dominance after clearing invasive alien plants in South Africa. Focus is placed on the definition, habits, biomes, target invaders, factors leading to, effects and management of secondary invasion and/or weedy native species dominance. Results suggest that secondary invasion and/or weedy native species dominance are often observed after clearing target invaders but is seldom reported, focused on, identified by name and/or correctly defined. The occurrence of secondary invasion and/or weedy native species dominance is not biome specific and is mediated by factors such as soil physico-chemical legacies of target invaders, availability of propagules in the soil seed bank and surrounding areas, and side effects of the technique used to clear target invaders. Ferns, grasses, herbs, sedges, shrubs, and trees can be secondary invaders and/or weedy native species. Few or no management interventions currently target secondary invasion and/or weedy native species dominance in South Africa. Given the paucity of knowledge on secondary invasion and/or weedy native species dominance in South Africa, there is clearly a need for more research. Practitioners should integrate the management of secondary invasion and/or weedy native species dominance with their overall invasive alien plant clearing efforts. Relevant steps should be taken to include mechanisms and incentives of dealing with secondary invasion and/or weedy native species dominance in the policy on invasive alien plants in South Africa.

1. Introduction

Invasive alien plants commonly exert negative ecological impacts on the ecosystems they invade, disrupt ecosystem services and impose a significant cost to the global economy (Pejchar and Mooney, 2009; Vilà et al., 2010, 2011). Management of invasive alien plants is necessary to mitigate these negative impacts (ordinarily this involves their removal from invaded ecosystems) and promote native biodiversity recovery (Hulme, 2006; Pyšek and Richardson, 2010). It is often assumed that native biodiversity recovery will follow the removal of invasive alien plants from invaded ecosystems (Wittenberg and Cock, 2005; Blanchard and Holmes, 2008). However, invasive alien plant management is inherently complex, and it is well known that the removal of invaders may not always translate to full or even partial recovery of native biodiversity (Zavaleta et al., 2001; Pearson et al., 2016; Mangachena and Geerts, 2017, 2019).

Various reasons have been proposed for the lack of full or partial recovery of native biodiversity after clearing invasive alien plants, e.g. soil legacy effects (Corbin and D'Antonio, 2012), depleted native soil seed banks (Le Maitre et al., 2011), re-invasion (Richardson and Kluge, 2008), secondary invasion and/or weedy native species dominance (Pearson et al., 2016; Nsikani et al., 2018b). Secondary invasion has been broadly defined as the proliferation of non-target alien species following efforts to suppress dominant target invaders (Pearson et al., 2016; Nsikani et al., 2018b; Nsikani et al., 2019). Secondary invasion has also been narrowly defined as a phenomenon where the invasion success of one invasive species (the secondary invader) is contingent on the presence, influence, and impact of one or more other invasive species (target invaders) (O'Loughlin and Green,

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https://doi.org/10.1016/j.sajb.2020.05.009
0254-6299/

2017). Here, we follow the broader definition since merits of the narrower definition have been discredited by Pearson et al. (2018). Weedy native species dominance has been broadly defined as the proliferation of native species that are not typically found and desired in the target area, and have detectable impacts (Pyšek et al., 2004; Nsikani et al., 2017, 2018b). Weedy native species dominance can occur without prior invasion and management of target alien invasive plants. This is because the proliferation of weedy native species can be facilitated by other anthropogenic factors such as fire, road construction and maintenance, and overgrazing (DiTomaso, 2000; Larson, 2002). However, here we focus on weedy native species dominance following invasion and management of alien invasive plants – i.e. following the creation of a 'weed-shaped hole' in disturbed ecosystems (Buckley et al., 2007).

The main prerequisite for secondary invasion and/or weedy native species dominance is the removal of target invaders since it creates "space" by decreasing competition and increasing the availability of resources, particularly soil nutrients (Buckley et al., 2007; Kettenring and Adams, 2011). Secondary invaders and/or weedy native species in turn occupy this space as their propagules move in from surrounding areas or were already present in the soil seed bank before clearing the target invaders (Gioria et al., 2014; Nsikani et al., 2018b). Secondary invasion and/or weedy native species dominance can be further exacerbated by: (1) persistent target invader soil legacies – e.g. elevated soil nutrient levels (Yelenik et al., 2004; Von Holle et al., 2013; Grove et al., 2015); (2) side effects of the technique used to clear target invaders – e.g. "fell, stack and burn" clearing method (felling target invaders, stacking the slash and allowing it to dry before burning it) which is known to elevate soil nutrient availability and scarify seeds to the benefit of secondary invaders and/or weedy native species in the burnt areas (Skurski et al., 2013; Nsikani et al., 2019); (3) provenance effects – i.e. secondary invaders and/or weedy native species often possess "weedy" or disturbance-adapted traits that are favoured during the introduction process after clearing target invaders (Pearson et al., 2014; Buckley and Catford, 2016); and (4) anthropogenic activities – e.g. altered disturbance regimes, eutrophication and global climate change can change environmental conditions or resource availability to favour secondary invasion and/or weedy native species dominance (MacDougall and Turkington, 2005; Bauer and Reynolds, 2016). Once most secondary invaders and/or weedy native species are present in a cleared area, their proliferation is aided by their ability to establish rapidly (O'Loughlin and Green, 2017; Torres et al., 2018). Secondary invaders and weedy native species can often co-exist at the same site after clearing target invaders (Nsikani et al., 2017, 2018b). Such co-existence between secondary invaders and weedy native species could be the result of direct (e.g., due to the increase in resources such as nutrients that can be shared between species) and indirect (e.g. due to suppression of a shared competitor) facilitation between plants (Flory and Bauer, 2014).

Secondary invasion and/or weedy native species dominance can present significant barriers to the conservation of native ecosystems under threat from invasive alien plants (Pearson et al., 2016; Nsikani et al., 2018b). It is common for secondary invaders and/or weedy native species to dominate areas cleared of target invaders for extended periods and to exert their own range of impacts, thereby hindering restoration by severely limiting the recovery of target native biodiversity (Symstad, 2004; Yelenik et al., 2004; Loh and Daehler, 2008; Nsikani et al., 2018a, 2019; Torres et al., 2018). However, secondary invasion and/or weedy native species dominance may decline following re-invasion or recovery of native biodiversity (Kettenring and Adams, 2011; Pearson et al., 2016; Nsikani et al., 2018b).

The establishment of secondary invaders and/or weedy native species can be reduced through soil solarization (heating the soil surface by covering with a plastic sheet) or setting up weed mats (woven plastic mats that allow passage of water but prevent emergence of seedlings) after clearing target invaders (Pickart et al., 1998; Cohen et al., 2008). Secondary invaders and/or weedy native species that establish can be controlled through herbicide application, manual weeding, mowing or selective grazing (Maron and Jefferies, 2001; Gooden et al., 2009; Milchunas et al., 2011; Szitár et al., 2016). Because secondary invaders and/or weedy native species often prefer high soil nitrogen availability, reduction of nitrogen levels can reduce their abundance (Alpert and Maron, 2000; Yelenik et al., 2004; Kulmatiski, 2011). Revegetation of the cleared site with typical native species is the most crucial management tool, since the space created by clearing target invaders is the main prerequisite for secondary invasion and/or weedy native species dominance (Buckley et al., 2007; Kettenring and Adams, 2011; Cutting and Hough-Goldstein, 2013). However, revegetation efforts currently appear to be largely unsuccessful (Kettenring and Adams, 2011), probably because secondary invaders and/or weedy native species outcompete target native species (Nsikani et al., 2018b). This problem calls for an integrated management approach for dealing with secondary invasion and/or weedy native species dominance (Nsikani et al., 2018b).

The threat of secondary invasion and/or weedy native species dominance is a ubiquitous problem. A growing number of studies have documented secondary invasion and/or weedy native species dominance across a range of ecosystems and countries (e.g. Richardson et al., 2000a; Symstad, 2004; Yelenik et al., 2004; Loh and Daehler, 2008; Skurski et al., 2013; Nsikani et al., 2018a, 2019; Torres et al., 2018). Efforts have been made to review the literature at a global level (e.g. Kettenring and Adams, 2011; Pearson et al., 2016) and at country-specific level, e.g. for Australia (Reid et al., 2009) and the United States of America (USA; Abella, 2014). However, global reviews have failed to produce an accurate review of secondary invasion and/or weedy native species dominance in South Africa (Appendix A). For example, the most recent global review by Pearson et al. (2016) included only two South African studies. Furthermore, no country-specific review has been conducted on secondary invasion and/or weedy native species dominance in South Africa, despite a growing number of such studies (Appendix A).

In this study, we have taken a two-pronged approach – a literature review plus a participatory interactive expert workshop – to evaluate the knowledge on secondary invasion and/or weedy native species dominance in South Africa. We aim to (1) determine how secondary invasion and/or weedy native species dominance have been defined in South Africa; (2) identify habits of secondary invaders and/or weedy native species; (3) identify biomes where secondary invasion and/or weedy native species dominance have been observed; (4) identify the target invaders that were cleared before secondary invasion and/or weedy native species dominance; (5) determine the factors that facilitated secondary invasion and/or weedy native species dominance; (6) determine the effects of secondary invasion and/or weedy native species dominance; (7) identify management approaches for secondary invasion and/or weedy native species dominance and evaluate their outcomes; and (8) provide management and research recommendations on secondary invasion and/or weedy native species dominance.

2. Methods

2.1. Literature review

We searched Google Scholar (http://scholar.google.com) and ISI Web of Science (http://apps.webofknowledge.com) with no restriction on publication date up to January 2020. From this we generated a database of published studies on secondary invasion and/or weedy native species dominance after clearing target invaders in South Africa. We used the following search terms: "exotic" OR "invasive" OR "invasion" OR "invad*" OR "alien" OR "non-native" AND "secondary inva*" OR "invasion meltdown" OR "weedy native" OR "weed" OR

"weedy species" OR "nitrophilic" AND "South Africa". Abstracts of retrieved articles were read and those relevant to the study were selected. References of included articles were screened for other relevant publications.

2.2. Workshop on secondary invasion in South Africa with researchers and practitioners working on invasive alien plants

We held a workshop on secondary invasion in South Africa with researchers and practitioners working on invasive alien plants at the 46th National Symposium on Biological Invasions in Tulbagh, Western Cape, South Africa (16 May 2019) (https://sites.google.com/view/biological-invasions-symposium/home). The workshop was attended by 52 participants, mostly researchers, and lasted for two hours. The workshop participants were from the Agricultural Research Council, CapeNature, Centre for Biological Control, Centre for Invasion Biology, Department of Environment, Forestry and Fisheries (particularly people working in the Natural Resources Management programme), South African National Biodiversity Institute and several universities in the country. The lead author facilitated the workshop with the help of the three co-authors. The facilitator began the workshop with a 10-min presentation summarising the South African literature on secondary invasion. The floor was then opened for participative discussions on: (1) the definition of secondary invasion (15 min); (2) observed cases of secondary invasion (10 min); (3) factors leading to secondary invasion (25 min); (4) effects of secondary invasion (20 min); (5) management approaches for secondary invasion and their outcomes (20 min); and (6) management and research recommendations on secondary invasion (20 min). During each point of discussion, time was allocated to clarifying relevant concepts, identifying and discussing alternative views, sharing of experiences by the participants and/or reaching consensus on relevant aspects. The workshop facilitator and one co-facilitator took notes during the discussions. The discussions were recorded for reviewing after the workshop to ensure that deliberations were accurately captured. Here, we present a summary of the discussions at the workshop based on the recordings, notes taken during the workshop, and discussions among the co-authors. We particularly highlight the aspects of the discussions where consensus was reached by the workshop and where differences in opinion were raised.

3. Results

We identified 28 papers (20 on secondary invasion, one on weedy native species dominance and seven discussing both secondary invasion and weedy native species dominance) that were relevant to this review (Appendix A). Twenty-two studies were conducted within one to 22 years after clearing, four studies were done in areas still occupied by target invaders and two were reviews (Appendix B).

3.1. Definition of secondary invasion and weedy native species dominance

3.1.1. Literature review

Studies on secondary invasion mostly identified the phenomenon by name (67%) while only half the studies on weedy native species dominance identified it by name (Fig. 1(A)). Studies on secondary invasion often did not (52%) or incorrectly define it (26%) (Fig. 1(B)). Similarly, studies on weedy native species dominance often did not (50%) or incorrectly define it (13%) (Fig. 1(B)).

3.1.2. Workshop

The workshop participants identified that secondary invasion is often observed after clearing target invaders but seldom focused on, identified by name and/or correctly defined in studies conducted in those areas. The workshop established that more research on secondary invasion after clearing target invaders is required and that secondary invaders species should be identified to species level in such studies. Participants agreed that the correct definition of secondary invasion is "the proliferation of non-target alien species following efforts to suppress dominant target invaders" (Pearson et al., 2016). The definition of secondary invasion by O'Loughlin and Green (2017) – a phenomenon where the invasion success of one invasive species (the secondary invader) is contingent on the presence, influence, and impact of one or more other invasive species (target invaders), was rejected. The workshop recognised that the problem of misuse of existing terminology extends beyond secondary invasion to numerous occurrences and concepts in invasion science and ecology in general (Richardson et al., 2000b; Hodges, 2008). The inevitability of subjectivity in invasion science research was recognised (Colautti and Richardson, 2009). Therefore, researchers and practitioners working on invasive alien plants were encouraged to use the definition of secondary invasion indicated above or variations of it, provided that the main message of proliferation of other alien species after clearing target invaders is not lost.

3.2. Habits of secondary invaders and/or weedy native species, and biomes where they were observed

3.2.1. Literature review

Secondary invaders were mostly grasses (78% of studies) and herbs (63% of studies), followed by shrubs (26% of studies), trees (22% of studies) and sedges (4% of studies) (Fig. 2). Examples of secondary invaders that were identified include *Briza maxima* L., *Bromus diandrus* Roth, *Conyza sumatrensis* (Retz.) E. Walker, *Hypochoeris radicata* L., *Lantana camara* L., *Raphanus raphanistrum* L. and *Rapistrum rugosum* (L.) All.. Weedy native species were found to comprise mostly grasses (88% of studies) and some ferns (13% of studies) (Fig. 2). Examples of weedy native species that were identified include *Cynodon dactylon* (L.) Pers., *Ehrharta calycina* Sm. and *Pteridium aquilinum* (L.) Kuhn. Biomes where the studies were conducted include fynbos (96%), forest (11%), savanna (4%), karoo (7%) and grassland (4%) (Fig. 3).

3.2.2. Workshop

The workshop recognised that grasses, herbs, shrubs and trees can be secondary invaders after clearing target invaders. Grasses and herbs were identified as the most common secondary invaders. Discussions at the workshop covered secondary invasion in fynbos, grassland, forest and thicket biomes, because the participants worked in or had experience of these biomes.

3.3. Target invaders that were cleared before secondary invasion and/or weedy native species dominance

3.3.1. Literature review

Secondary invasion was dominant following the clearing of 14 target invader species while weedy native species was dominant following the clearing of 8 target invader species (Table 1). Target invader species were mostly trees (12 species) but also included a grass and a herb (Table 1). A majority (8 species) did not possess the ability to fix nitrogen (Table 1). *Acacia saligna* was the most common target invader species that led to both secondary invasion (52% of studies) and weedy native species dominance (50% of studies) (Table 1). In fact, most target invader species belonged to the genera *Acacia* (4) and *Eucalyptus* (5) (Table 1).

3.3.2. Workshop

The workshop identified that secondary invasion has often been observed following the clearing of invasive alien trees, particularly, invasive Australian acacias.

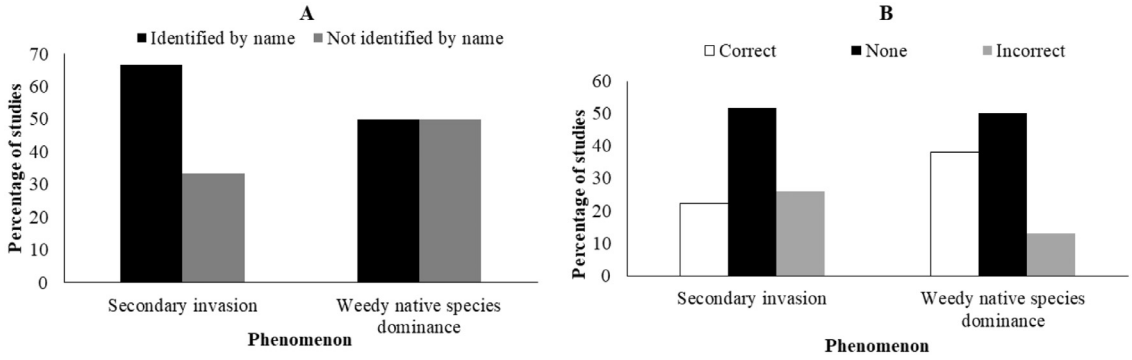

Fig. 1. Percentage of studies on secondary invasion (n = 27) and weedy native species dominance (n = 8) in South Africa that either identified each phenomenon by name or not (A) and provided correct, incorrect or no definition of each phenomenon (B).

3.4. Factors that facilitate secondary invasion and/or weedy native species dominance

3.4.1. Literature review

All studies provided factors giving rise to secondary invasion and/or weedy native species dominance, except for three (Appendix B). Four factors were identified as leading to secondary invasion and/or weedy native species dominance and were directly tested by at least one study: (1) soil physico-chemical legacies of target invaders (72% of studies); (2) availability of propagules in the soil seedbank or surrounding areas (32% of studies); (3) side effects of the technique used to clear target invaders (i.e. technique creates conditions that favour secondary invasion and/or weedy native species dominance) (14% of studies); and (4) reduced competition from target invaders and native species (11% of studies) (Appendix B). Five factors were identified as leading to secondary invasion and/or weedy native species dominance but were not directly tested in any study: (1) light availability (7% of studies); (2) anthropogenic activities (7% of studies); (3) disturbances that lead to availability of resources (4% of studies); (4) provenance effects (4% of studies); and (5) appropriate germination conditions (4% of studies) (Appendix B).

3.4.2. Workshop

Participants agreed that clearing target invaders led to secondary invasion since it created space by removing the dominant and highly competitive target invaders. The presence of secondary invader propagules in cleared sites or surrounding areas was identified as a crucial factor mediating their establishment. Soil chemical legacies of target invaders such as elevated soil nutrients (mostly nitrogen), were identified as the main factor facilitating the proliferation of secondary invaders once they are established. Therefore, secondary invasion after clearing nitrogen-fixing target invaders such as Australian acacias was thought to be more prevalent than after removal of non-nitrogen fixing invaders. The presence of target invader biomass on-site after initial and follow-up target invader clearing was also identified as causing elevated soil nitrogen availability, thereby facilitating secondary invasion. Side effects of the technique used to clear target invaders were also recognised as facilitating secondary invasion. Firstly, the use of the "fell, stack and burn" clearing method (see Holmes et al., 2020 for details) was considered to elevate soil nitrogen availability in burnt areas, thereby leading to an increase in secondary invasion (Nsikani et al., 2019). Burning of stacks was also said to stimulate germination of fire-cued secondary invaders (Nsikani et al., 2019). Secondly, the use of broadleaf herbicides during initial or follow-up clearing was said to favour the proliferation of secondary invader grasses while suppressing native monocots and/or dicots (Pearson et al., 2016; Nsikani et al., 2019).

3.5. Effects of secondary invasion and/or weedy native species dominance

3.5.1. Literature review

Reduced native species recovery through competition for resources was identified (in 82% of studies) as an effect of secondary

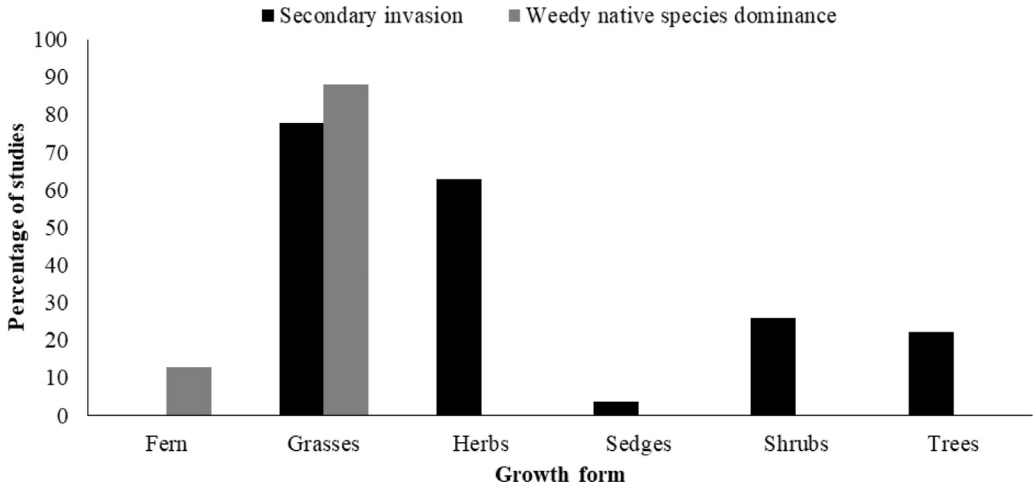

Fig. 2. Percentage of studies on secondary invasion (n = 27) and weedy native species dominance (n = 8) in South Africa that identified ferns, grasses, herbs, sedges, shrubs and trees as secondary invaders and/or weedy native species.

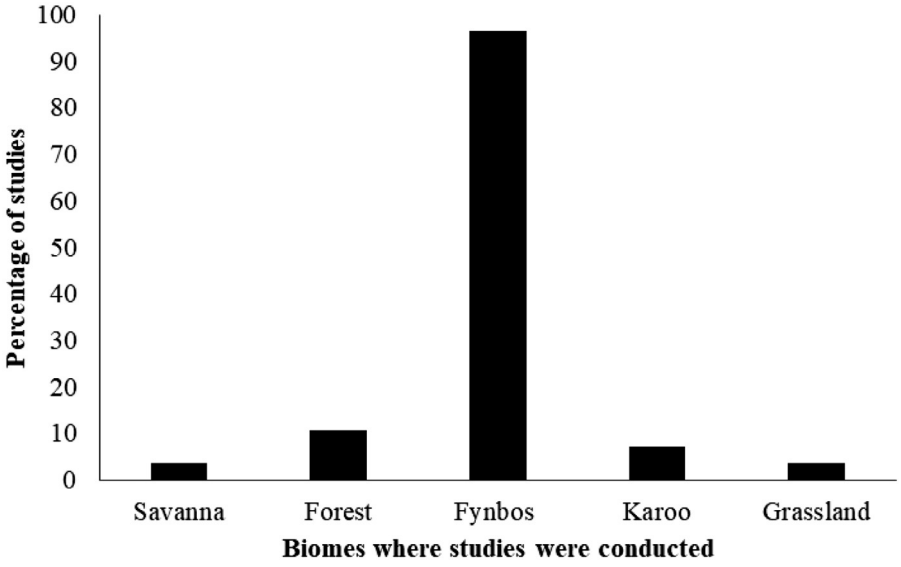

Fig. 3. Biomes where studies (n = 28) on secondary invasion and weedy native species dominance were conducted in South Africa, and the percentage of studies conducted in each biome. Karoo includes both the Nama and Succulent Karoo.

invasion and/or weedy native species dominance and directly tested by at least one study (Appendix B). Two effects of secondary invasion and/or weedy native species dominance were identified but not directly tested by any study: (1) changes in ecosystem services (4% of studies); and (2) altered fire dynamics (4% of studies) (Appendix B).

3.5.2. Workshop

The workshop recognised that the nature and severity of the effects of secondary invasion are context-dependent, e.g. type of secondary invaders. However, despite the context, secondary invasion hinders native species recovery. There was general agreement that secondary invasion can result in the continuation of some of the impacts generated by the target invaders in the ecosystem, e.g. elevated soil nitrogen availability (Nsikani et al., 2017), and that failure to deal with secondary invaders in some cases annulled the gains and benefits achieved by clearing target invaders. There was disagreement as to whether secondary invaders can also have positive impacts, e.g. act as nurse plants for recovering native species.

3.6. Current management approaches for secondary invasion and/or weedy native species dominance and their outcomes

3.6.1. Literature review

Only one study managed secondary invasion, and none managed weedy native species dominance. Holmes (2005) used ploughing during clearing of the target invader *Medicago sativa*, which led to a significant reduction in the establishment of secondary invaders compared to areas that were not ploughed.

3.6.2. Workshop

Workshop participants agreed that currently there are little or no management efforts targeting secondary invasion in South African ecosystems. It was recognised that management efforts currently only concentrate on initial and follow-up clearing of target invaders and largely ignore secondary invasion. This was mainly attributed to the current policy regulating alien species in South Africa, i.e. National Environmental Management: Biodiversity Act ([NEMBA 2004] Act 10 of 2004), which lists alien plants requiring management

Table 1
Target invader species whose clearing was followed by secondary invasion and weedy native species dominance in South Africa, their relevant characteristics and the percentage of studies (secondary invasion: n = 27; weedy native species dominance: n = 8) recording the target invaders.

Species	Secondary invasion (% of studies)	Weedy native species dominance (% of studies)	Growth form	Nitrogen-fixing ability
Acacia saligna (Labill.) H.L.Wendl.	52	50	Tree	Yes
Acacia mearnsii De Wild.	26	25	Tree	Yes
Acacia longifolia (Andr.) Willd.	26	0	Tree	Yes
Eucalyptus camaldulensis Dehnh.	22	0	Tree	No
Eucalyptus cladocalyx F. Muell.	7	13	Tree	No
Eucalyptus grandis W.Hill	7	13	Tree	No
Pennisetum clandestinum Hochst. ex Chiov.	7	0	Grass	No
Pinus radiata D.Don	7	0	Tree	No
Acacia melanoxylon R.Br.	4	13	Tree	Yes
Lupinus luteus L.	4	13	Tree	Yes
Medicago sativa L.	4	13	Herb	Yes
Pinus pinaster Aiton	4	13	Tree	No
Eucalyptus conferruminata D.J.Carr & S.G.M.Carr	4	0	Tree	No
Eucalyptus gomphocephala DC.	4	0	Tree	No

(van Wilgen, 2012). Most secondary invaders are not included on these lists since they are not considered as high-impact weeds. Practitioners are therefore not obliged to manage them. In fact, it is common for practitioners to assume that secondary invasion is not a problem. This is partly due to the lack of awareness and knowledge among researchers and practitioners working on invasive alien plants in South Africa. Participants highlighted that even when practitioners recognise the need to manage secondary invasion, their budgets do not allow for this, and if they do, it entails a lengthy process. Workshop participants disagreed on the extent to which secondary invasion can lead to arrested succession – a situation when early- and mid-successional species dominate the community so that later successional species are suppressed, and succession is strongly delayed or practically stopped (Young and Peffer, 2010). Some of the workshop participants expressed the strong view that secondary invaders give way to native species after a few years, therefore, their management is not warranted. However, there is currently no strong evidence from the global literature to support this opinion.

3.7. Management and research recommendations on secondary invasion and/or weedy native species dominance

3.7.1. Literature review

Seven management recommendations on secondary invasion and/or weedy native species dominance in South Africa have been proposed in the literature: (1) effective follow-up clearing targeting secondary invaders and/or weedy native species through herbicide application, grazing, manual weeding, mowing and/or prescribed burning (50% of studies); (2) management of soil chemical legacies of target invaders through carbon application, fire and/or planting of typical native species adapted to low N availability (25% of studies); (3) restoration of key native species through the sowing of seed and/or planting of seedlings (21% studies); (4) effective long-term monitoring (18% of studies); (5) reduction in the establishment of secondary invaders and/or weedy native species through soil transfer, ploughing, soil solarization and/or weed mats (11% of studies); (6) thinning of target invaders instead of complete clearing (11% of studies); and (7) spreading of the slash of target invaders across the restoration site after clearing instead of stacking and burning (4% of studies) to prevent elevated soil nitrogen availability (Appendix B). Four aspects were recommended for further research: (1) effects of secondary invasion and/or weedy native species dominance on typical native species recovery (11% of studies); (2) soil chemical legacies of target invaders (7% of studies); (3) effects of target invader soil chemical legacies on secondary invasion and/or weedy native species (4% of studies); and (4) factors facilitating the proliferation of secondary invaders and/or weedy native species (4% of studies) (Appendix B).

3.7.2. Workshop

Workshop participants agreed that revegetation of cleared sites with native species through seed and/or plantings can reduce secondary invasion. There was discussion about cautiously planning revegetation efforts after clearing target invaders and that specific goals should be defined from the onset – e.g. restoration vs. rehabilitation. The workshop recognised that revegetation through passive means may not be adequate given the common challenge of depleted native soil seed banks after clearing target invaders. Active revegetation may therefore be desirable, but such actions are often constrained by scale and finances. There was agreement that the management of secondary invasion must be context-dependent and may be easier in some biomes compared to others, e.g. forests vs. fynbos (Nsikani et al., 2018b). The workshop agreed that there is need to investigate: (1) conditions that can lead to secondary invasion after clearing target invaders; (2) species that could become secondary invaders after clearing target invaders; (3) the effects of secondary invasion beyond native species recovery, e.g. fire regimes, soil chemical and biotic composition; and (4) management options for secondary invasion.

4. Discussion

The phenomena of secondary invasion and weedy native species dominance after clearing target invaders have not been widely reported in the South African literature as shown by the small number of studies selected for this review (28) and the discussions at our workshop. Many aspects are only described by a few studies and there is a strong bias in favour of a few biomes, notably the fynbos. We believe that this is in no way an affirmation that ecosystems in South African are less at risk from secondary invasion and/or weedy native species dominance than those in countries such as Australia and the USA where the phenomenon has been more comprehensively documented (Reid et al., 2009; Abella, 2014; Nsikani et al., 2018b). Rather, it is an indictment of the current research, management and policy on invasive plants in South Africa, which largely ignores secondary invaders and/or weedy native species. Furthermore, the bias in favour of the fynbos biome in the literature review and discussions at our workshop is an accurate reflection of the trends in biological invasions research in South Africa; the fynbos is the most studied biome when it comes to invasive plants and their management (Richardson and van Wilgen 2004; van Wilgen et al., 2020). South Africa is however not unique in giving limited attention to secondary invasion and/or weedy native species dominance, because recent global reviews have shown that most literature on secondary invasion and/or weedy native comes from work in the USA and, to a lesser extent, Australia (Kettenring and Adams, 2011; Pearson et al., 2016; Nsikani et al., 2018b).

We concede that our workshop could have benefitted from including weedy native species dominance in the discussions rather than focussing only on secondary invasion. However, we believe that most, if not all, of the aspects on secondary invasion raised at the workshop equally apply to weedy native species dominance. This is because factors leading to and exacerbating the effects of secondary invasion as well as interventions to manage them, are similar to those that drive weedy native species dominance (Nsikani et al., 2018b). In fact, the decision to include weedy native species dominance in the literature review was a product of the discussions at our workshop which highlighted the similarities in causes, consequences and management of secondary invasion and weedy native species dominance.

Considerable focus has understandably been on dealing with target invasive alien plants and their management as there are 317 such species listed in national legislation and for which management action is mandated (Richardson et al. 2020). Also, given the importance of native species recovery after managing target invaders, focus has understandably been skewed towards native species dynamics (Holmes et al., 2020), despite a range of secondary invaders and/or weedy native species that have increasingly been observed in previously invaded areas (e.g. Richardson et al., 2000a; Yelenik et al., 2004; Blanchard and Holmes, 2008; Gaertner et al., 2011, 2012; Fill et al., 2018; Nsikani et al., 2018a, 2019). Often, policy makers, researchers and practitioners do not recognise secondary invasion and/or weedy native species dominance as important barriers to native biodiversity recovery which can potentially reverse the gains achieved by clearing target invaders (Kettenring and Adams, 2011; Pearson et al., 2016; Nsikani et al., 2018b). If practitioners do recognise the need to manage secondary invasion and/or weedy native species dominance in their areas, they may often be financially incapacitated to do so or take too long to respond.

Weedy native species are often considered to cause less harm (or no harm) since they are native to the country and/or the habitat under consideration, despite their weedy nature (Yelenik et al., 2004; Reinecke et al., 2008; Nsikani et al., 2018a, 2018b). This widely held opinion is probably why our results show a disproportionate research

intensity between secondary invasion and weedy native species dominance, with the former being favoured. Recent studies have shown that such a bias also exists in the global literature on secondary invasion and/or weedy native species dominance (Nsikani et al., 2018b) and the global study of alien and/or native invasive species (Nackley et al., 2017).

Current policy on invasive plant management in South Africa focuses heavily on target alien invaders and their management, but lacks clear mechanisms and incentives to deal with secondary invaders and/or weedy native species, particularly those that are not already recognised as target invaders elsewhere (van Wilgen and Wilson, 2018). In fact, the policy on invasive plants in South Africa is largely silent when it comes to secondary invasion and/or weedy native species dominance (van Wilgen and Wilson, 2018), though in some cases secondary invaders that are listed in the national invasive species list tend to be removed during follow-up clearing. We suspect that the limited knowledge on secondary invasion and/or weedy native species dominance – as evidenced by the small number of studies included in this review and the discussions at our workshop – could be the main reason why they are not clearly addressed by the policy on invasive plants in South Africa. The lack of comprehensive formal national, provincial and/or biome-specific noxious weed lists (covering both native and alien species) in South Africa (such as are available for other countries, for instance the USA and Canada; Skinner et al., 2000) is probably another reason for the lack of a clear policy, limited recognition, research and management of secondary invasion and weedy native species dominance (Richardson et al., 2020).

Our literature review shows that the misidentification of secondary invaders and weedy native species has been widespread in South Africa; this has led to some species being wrongly classified as secondary invaders or weedy native species. This is probably not a result of a failure to accurately identify alien or native species as is sometimes the case elsewhere (e.g. North America and Europe; Webber and Scott, 2012; Hill and Hadly, 2018), but a lack of clarity regarding the concept of secondary invasion or invaders. While the definition of a weedy species (native or alien) has long been agreed upon (Baker, 1974), the debate on the definition of a secondary invader has only recently been settled (Pearson et al., 2016; O'Loughlin and Green, 2017; Pearson et al., 2018). It is worth noting that grasses are the most important growth form in secondary invasion and/or weedy native species dominance in South Africa; grasses comprise an overwhelming majority of and are the only common growth form between secondary invaders and weedy native species. This mirrors the situation in the USA and Australia, especially in situations when herbicides were used to control target invaders (Reid et al., 2009; Pearson et al., 2016; Nsikani et al., 2018b). Overall, the causes, consequences and management of secondary invasion and/or weedy native species dominance found in our study are similar to those found globally (reviewed in Kettenring and Adams, 2011; Pearson et al., 2016; Nsikani et al., 2018b).

4.1. The way forward

We urge policy makers, researchers and practitioners working on invasive plants in South Africa to recognise that secondary invasion and/or weedy native species dominance can act as a barrier to target native biodiversity recovery and reverse gains achieved by clearing target invaders (Nsikani et al., 2018b). These secondary invaders and/or weedy native species can be of any growth form (i.e. ferns, grasses, herbs, sedges, shrubs and trees). Although beyond the scope of this study, it is worth noting that hydrophytes can also be secondary invaders and/or weedy native species in aquatic systems (Strange et al., 2019). Whenever possible, secondary invaders and/or weedy native species that assume dominance should be clearly identified to species level. Policy makers, researchers and practitioners must ensure that they correctly define and describe secondary invasion (the proliferation of non-target alien species following efforts to suppress dominant target invaders) and/or weedy native species dominance (the proliferation of native species that are not typically found and wanted in the target area, and have detectable impacts) (Pyšek et al., 2004; Pearson et al., 2016; Nsikani et al., 2018b). Depending on the context, we encourage practitioners to manage secondary invasion and/or weedy native species dominance after clearing target invaders (Nsikani et al., 2018b).

Given the paucity of knowledge on secondary invasion and/or weedy native species dominance in South Africa, there is clearly need for more research to inform a policy shift towards appropriate management of secondary invaders and/or weedy native species. The creation and maintenance of comprehensive formal national, provincial and/or biome-specific noxious weed lists (covering both native and alien species) would ensure increased recognition of the growing problems with species in these categories. Such lists would be useful inputs to formal policies for dealing with them. Management options, factors leading to and effects of secondary invasion and/or weedy native species dominance identified in this review are largely untested. Researchers need to collaborate with practitioners to enhance our understanding of the drivers and impacts of secondary invasion and/or weedy native species dominance and explore the feasibility and effectiveness of different management strategies.

Declaration Competing of Interest

None.

Acknowledgments

Funding for this work was provided by the DSI-NRF Centre of Excellence for Invasion Biology. DMR also acknowledges support from the Oppenheimer Memorial Trust (grant 18576/03) and the National Research Foundation (grant 85417). We are sincerely grateful to everyone who participated in the workshop on secondary invasion in South Africa at the 46th National Symposium on Biological Invasions in Tulbagh, Western Cape.

Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.sajb.2020.05.009.

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